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SEROLOGICAL DIFFERENCES IN THE GENUS *PEROMYSCUS* DEMONSTRABLE WITH NORMAL HUMAN SERA

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INTRODUCTION

IN number of species and subspecies the rodent genus *Peromyscus* outranks all other mammalian genera of North America. Most of its species are easily reared in the laboratory, and some are known to produce fertile species hybrids under laboratory conditions (Dice, 1940). Such qualities make this group of exceptional value for the study of mammalian variation at the species and subspecies levels. A search for serological differences between various *Peromyscus* species has been initiated by Moody, using anti-*Peromyscus* immune sera of rabbits and various rodents. Differences in the serum proteins, such as were readily demonstrated between various rodent families and genera (Levine and Moody, 1939), could not be detected within the genus *Peromyscus* by means of ordinary precipitin tests. By means of the Schultz-Dale reaction, however, Moody (1940) was able to differentiate the serum of *P. maniculatus gracilis* from that of *P. gossypinus palmarius*. The same author has also reported (1941) the separation of *P. leucopus* and *P. maniculatus* by means of agglutination tests with absorbed sera of rabbits immunized against *Peromyscus* cells.

The present report deals with antigenic differences in *Peromyscus* erythrocytes which are demonstrable with normal human agglutinins. Although such preformed antibodies would not be expected to differentiate *Peromyscus* antigens as readily as would the immune antibodies employed by Moody, the results of the preliminary tests described herein suggest that considerable differentiation may actually be secured. The ready availability of human sera constitutes a decided practical advantage. Moreover, the antigens demonstrated by such sera are of added interest owing to the fact that some of them can be identified as related to the human isoagglutinogen B. Since the work of von Dungern and Hirschfeld (1911), it has been known that the B factor of human erythrocytes is represented by serologically similar substances in the red blood cells of many other mammals. Like the human group substance A, the B agglutinogen is therefore a heterophile antigen of widespread occurrence. In man, the alcohol-soluble B factor of the red blood cells is determined by a gene, which is an allele of those for the A and O substances, and a second pair of genes (the "secretor" and "nonsecretor" factors) determines its concomitant presence or absence in water-soluble form. A further study of the B-like antigens of *Peromyscus* should prove of interest in connection with the genetics and evolution of these substances.

Other human agglutinins which may serve for the separation of certain *Peromyscus* species are apparently present in most or all normal human sera, irrespective of blood group. These are therefore inactive against human red blood cells and are designated as heteroagglutinins.

The mice used in the investigation were mostly taken from stocks available in the Laboratory of Vertebrate Biology. I am especially indebted to Elizabeth Barto for collecting the blood samples and to Dr. Alexander S. Wiener, who provided the author with several testing sera and offered valuable suggestions. Paul A. Moody kindly donated several specimens of *P. gossypinus*. The study was supported in part by the Horace H. Rackham School of Graduate Studies.

MATERIALS AND METHODS

Eight species of *Peromyscus* are represented in the various tests to be described. Since F_1 hybrids of *maniculatus* and *polionotus* were available for testing, these two species were sampled somewhat more adequately than the others. The term cenospecies (Blair, 1943), used in the following list of species, corresponds essentially to the species group of previous authors.

Peromyscus

Subgenus *Haplomylomys*

eremicus cenospecies
    P. eremicus eremicus, from Carrizozo, New Mexico
crinitus cenospecies
    P. crinitus crinitus, from St. George, Utah

Subgenus *Peromyscus*

maniculatus cenospecies
    P. maniculatus exiguus, from San Martin Island, Baja California
    P. maniculatus blandus, from Alamagordo, New Mexico
    P. maniculatus (various subspecies, including complex hybrids of *artemisiae, bairdii, gambeli, nebrascensis, rubidus,* and *sonoriensis*)

P. polionotus leucocephalus, from Santa Rosa Island, Florida
P. polionotus (various subspecies, including complex hybrids of *albifrons, leucocephalus, polionotus,* and *rhoadsi*)
F_1 hybrids of *P. maniculatus* and *P. polionotus*

leucopus cenospecies
P. leucopus noveboracensis, from Ann Arbor, Michigan
P. gossypinus palmarius, from Seebring, Florida

truei cenospecies
P. nasutus nasutus, from Lincoln, New Mexico
P. truei truei, from Capitan Gap, New Mexico

In most cases, the samples of blood were obtained from animals which had been set aside for sacrifice. Under etherization the jugular veins were severed, and the blood was collected into small test tubes. After clotting, the cells were resuspended in saline and washed several times. In some tests, where small quantities of cell suspension were sufficient, one or two drops of blood were obtained from the tail.

Approximately 2 per cent suspensions of cells were used in the agglutination tests. One or two drops of cell suspensions were mixed with like volumes of testing fluid in 10-mm. test tubes, and the mixtures were allowed to stand at room temperature with occasional shaking. Readings were made at one hour. The agglutination reactions are recorded as –, ±, +, ++, +++, ++++, the last grade denoting a completely agglutinated cell mass that did not break up on moderate shaking. For the absorption experiments, small quantities of blood cells were measured with hemocytometer pipettes and diluted with saline as required. All absorptions were carried out for a period of one hour at room temperature. Human blood suspensions of groups O, A_1, A_2, and B, and of types M, MN, and N were employed as controls in all series of tests.

ABSORPTION EXPERIMENTS WITH GROUP-A SERA

Each sample of *Peromyscus* blood was routinely tested with a number of reagents ordinarily employed for the serological typing of human blood. These included human group-B (anti-A) sera, human group-A (anti-B) sera, and absorbed rabbit antisera specific for the human agglutinogens A, B, M, and N. The results of such simple typing tests are summarized in Table I. The extent of agglutination recorded in this table represents the average reaction obtained with the several blood specimens of each species. Some quantitative variation within species was noted, but in no case did two individuals of the same species give completely different reactions, that is, one positive and the other negative.

The blood cells of all *Peromyscus* specimens were agglutinated by all human sera with the exception of two group-B sera (B–41 and B–518), which gave negative reactions with all *Peromyscus* bloods tested (Table I). A single serum of group O and one of group AB were also used in a part of the tests (not indicated in Table I) and were likewise found to possess agglutinins against all *Peromyscus* species. The two exceptional sera, B–41 and B–518, were of unusual origin and their significance will be discussed later. These being disregarded, it may best be considered that any human serum, regardless of blood group, may possess anti-*Peromyscus* agglutinins. This being the case, it is evident that the presence of A-like or B-like antigens cannot be established by the use of untreated human sera. It is shown in the following section, however, that a B-like substance is definitely present in species *maniculatus, polionotus, leucopus,* and *gossypinus.* It is therefore of interest that the bloods of these species are not agglutinated by anti-human-B sera produced by rabbits. This result is identical with the findings of Landsteiner and Miller (1925) on the bloods of monkeys and other mammals possessing B-like factors. These authors showed that anti-human-B agglutinins of immune rabbit sera were reactive with the cells of certain (group-B) apes and men, but not with monkeys and other mammals possessing a B-like antigen. The B factor of the higher primates is thus distinguishable from that of other mammals. According to Friedenreich and With's (1933) theory on the multiplicity of B components, these facts are explained by assuming that the human B agglutinogen contains a component shared by certain apes but not by *Peromyscus* and other mammals.

TABLE I

AGGLUTINATION REACTIONS OF THE CELLS OF SEVERAL *PEROMYSCUS* SPECIES

Species	No. of Bloods Tested	Normal Human Sera			Immune Rabbit Sera			
		Group B (most)	B–41 and B–518	Group A	Anti-A	Anti-B	Anti-M	Anti-N
leucopus	3	++++	−	++++	−	−	−	−
gossypinus	2	++++	−	++++	−	−	−	−
maniculatus	17	++++	−	++++	−	−	−	−
F$_1$ *maniculatus* × *polionotus* hybrids	7	++++	−	++++	−	−	−	−
polionotus	12	++++	−	++++	−	−	−	−
nasutus	6	±	−	±	−	−	−	−
truei	3	±	−	±	−	−	−	−
eremicus	9	++	−	++	−	−	−	−
crinitus	3	+	−	+	−	−	−	−

The finding that *Peromyscus* cells are not reactive with anti-M and anti-N rabbit agglutinins also agrees with the observations of Landsteiner and Miller, whose studies indicate that these properties are possibly restricted to the blood of man, apes, and certain monkeys.

Cells of the *Peromyscus* species *maniculatus, polionotus, leucopus,* and *gossypinus* were much more strongly agglutinated by untreated human sera than were those of species *nasutus, truei, eremicus,* and *crinitus* (Table I). These results recommended the trial of absorption methods for the purpose of securing reagents which might effect a qualitative separation of certain species. One such experiment, involving the use of five human group-B and thirty-two *Peromyscus* bloods, is summarized in Table II. For this experiment, a human group-A serum of high isoagglutinin titer (1024) was selected. Parts of this serum, diluted 1 : 16, were absorbed with one-tenth volumes of washed, packed cells of the thirty-seven bloods. Each of these preparations was then tested against cells of the same series of bloods. The average degree of agglutination within sets of readings involving test cells and absorbing cells of the same species is shown in Table II. Variation within species was again small as compared with the differences between species. Reactions recorded in Table II as ++++ were almost all complete agglutinations; reactions recorded as – were mostly negative with an occasional trace of agglutination (±); and reactions recorded as + or ++ were somewhat more variable.

Table II confirms Table I in showing a marked contrast between the cells of *maniculatus, polionotus,* F_1 *maniculatus* × *polionotus* hybrids, and *leucopus* and those of the species *nasutus, truei, eremicus,* and *crinitus.* Group-A serum exhausted of its agglutinins against any one of the species *nasutus, truei, eremicus,* or *crinitus* will readily distinguish cells of such species from those of *maniculatus, polionotus,* or *leucopus.* Furthermore, continued treatment of group-A sera with excesses of *nasutus, truei, eremicus,* or *crinitus* cells was found to be ineffective in removing the agglutinins against the remaining species. The results also suggested that further discrimination within the group *maniculatus, polionotus,* and *leucopus* should be possible with the aid of appropriately absorbed and diluted A sera. This possibility was tested by attempting to classify a series of fourteen bloods which were known only to comprise a collection of the three species, *maniculatus, polionotus,* and *eremicus.* By using *eremicus*-absorbed and *polionotus*-absorbed A serum, thirteen of these were correctly identified, the only error consisting in classifying a *maniculatus* blood as belonging to *polionotus.*

The experiment described in Table II involved a constant ratio between the volume of serum and the volume of absorbing cells. A number of tests were next performed using varying quantities for the absorptions. This was done with the view of determining the optimum proportion of absorbing cells for the preparation of a *polionotus*-absorbed serum with which to differentiate the species *maniculatus* and *polionotus* and also to determine whether larger quantities of the cells of these mice would exhaust the serum of its anti-human-B agglutinin. Figure 1 depicts the results of one such experiment comparing the absorptive capacities of *maniculatus, polionotus,* and human group-B cells. Parts of serum A–121, diluted 1 : 4, were absorbed with varying volumes of cells of these three species and then titrated against cells of each of the same three bloods. The titration curves against human group-B cells show that cells of the *maniculatus* mouse removed the β agglutinin about as rapidly as did human group-B cells. Furthermore, *polionotus* blood also removed the β agglutinin, although less effectively than *manicu-*

TABLE II

Agglutination of Five Human Group-B and Thirty-two *Peromyscus* Bloods with a Human Group-A Serum, before and after Absorption with Cells of the Same Individuals

Cells	No. of Bloods Tested	Serum A–121 1: 16 Unabsorbed	Serum A–121, 1: 16, Absorbed with 1/10 Vol. Cells of:								
			B	*l*	*m*	*mp*	*p*	*e*	*c*	*n*	*t*
Human group (B)	5	++++	+	++	+	±	++++	++++	++++	++++	++++
leucopus (*l*)	2	++++	++++	–	–	±	±	++++	++++	++++	++++
maniculatus (*m*)	6	++++	++++	–	–	–	++	++++	++++	++++	++++
F$_1$ *maniculatus* × *polionotus* hybrids (*mp*)	4	++++	++++	–	–	–	++	++++	++++	++++	++++
polionotus (*p*)	6	++++	++++	–	–	–	–	++++	++++	++++	++++
eremicus (*e*)	6	++	++	–	–	–	–	–	–	–	–
crinitus (*c*)	5	+	+	–	–	–	–	–	–	–	–
nasutus (*n*)	2	+	+	–	–	–	–	–	–	–	–
truei (*t*)	1	±	±	–	–	–	–	–	–	–	–

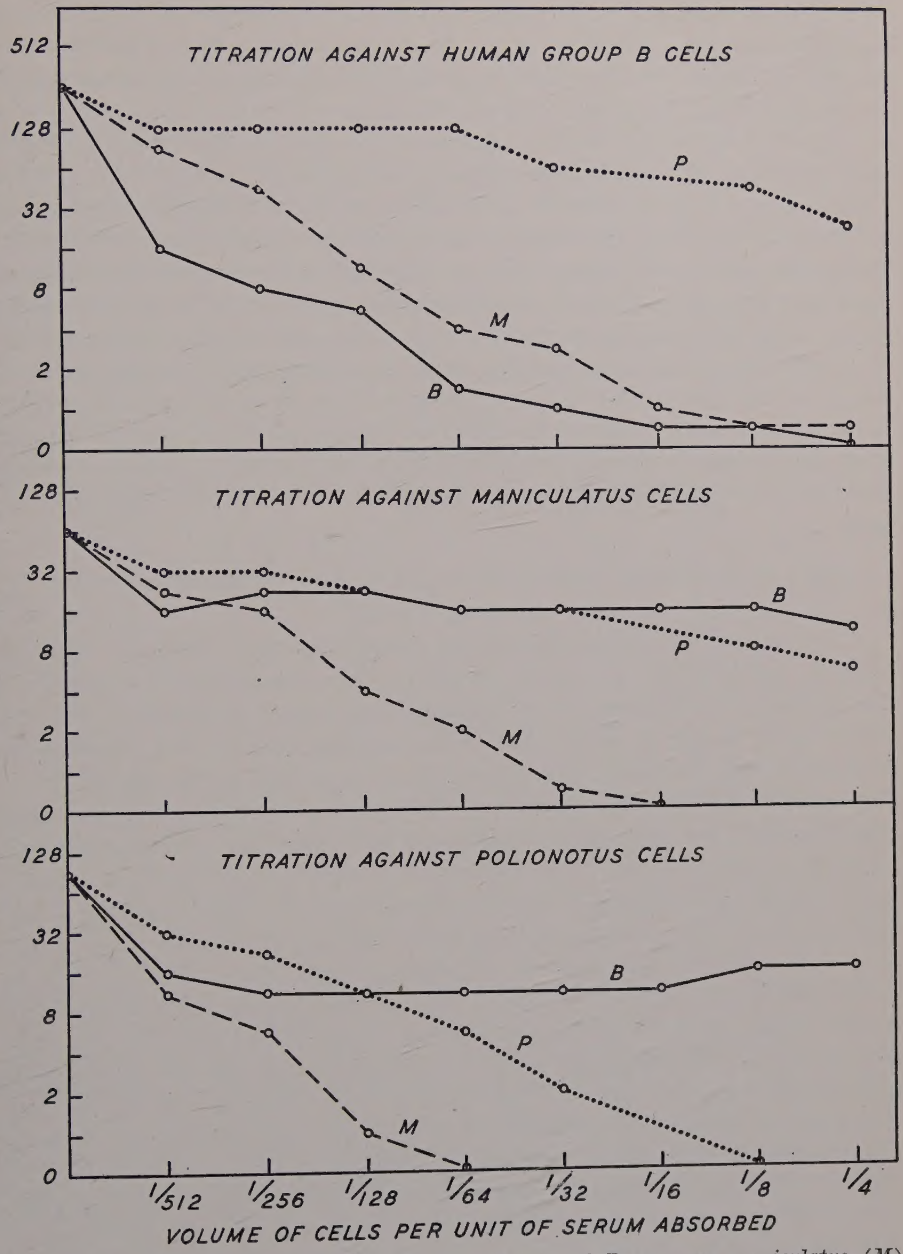

FIG. 1. Titration of serum A–121 against cells of *Peromyscus maniculatus* (*M*), *P. polionotus* (*P*), and human group B (*B*), after absorption with cells of the same three bloods.

latus, thus adding *polionotus* to the group of species suspected of possessing a B-like antigen. Whether the cells of *maniculatus* and *polionotus* are capable of completely absorbing the β agglutinin of group-A sera when used in larger quantities has not been ascertained.

Figure 1 further shows that human group-B cells were able to remove only a fraction of the anti-*Peromyscus* agglutinins, reducing the titer of the diluted A serum from about 64 to 16, after which excess B cells appeared to have no further effect. Such agglutinins, which remain in the human serum after exhaustion with human cells of homologous blood group, are termed heteroagglutinins and will be described further in the next section. Both anti-*maniculatus* and anti-*polionotus* agglutinins were removed more rapidly by *maniculatus* than by *polionotus* cells. According to this single series of tests, a group-A serum having an anti-*maniculatus* titer of 64 should provide the most satisfactory reagent for differentiating *maniculatus* and *polionotus* after absorption with one-fourth volume of *polionotus* cells. Titration curves similar to those of Figure 1 were obtained in tests with two other group-A sera.

TESTS WITH PURIFIED ISOAGGLUTININ β AND WITH HETEROAGGLUTININS OF GROUP-A SERA

The presence of a B-like antigen in *Peromyscus* cells of species *maniculatus,* F_1 *maniculatus* × *polionotus* hybrids, *polionotus,* and *leucopus* has been demonstrated by the capacity of these cells to reduce the titer of group-A sera against human B cells. A more decisive method for the detection of such substances, however, is considered to be furnished by the use of ''purified'' solutions of the isoagglutinin β. These are prepared by the process of ''splitting off'' the agglutinin bound to group-B cells that have been agglutinated by group-A serum. This method takes advantage of the fact that the isoagglutinins are released from the antigen-antibody complex by the application of heat. Three such solutions were prepared from different group-A sera, following the technique of Landsteiner and Miller (1925). Serum A–121 yielded the most concentrated solution, and the results of its titration against a small series of *Peromyscus* bloods are given in Table III. In addition to human cells of groups B and O, suspensions of two beef bloods were included as controls, since it is known that cattle possess a B-like antigen. Although the titers were smaller, the reactions of the two agglutinin solutions prepared from other sera were similar to those shown in Table III. Cells of *leucopus, gossypinus, maniculatus,* F_1 *maniculatus* × *polionotus* hybrids, and *polionotus* were all agglutinated about as strongly as human B cells, whereas cells of *nasutus, truei, eremicus,* and *crinitus* gave no trace of agglutination. The difference in reaction with untreated A sera in these two groups of species is thus shown to be due in large part to the presence or absence of a B-like antigen.

Exhaustive treatment of group-A sera with group-B cells separates the β isoagglutinin from other agglutinins which may activate the cells of other animals. Such "heteroagglutinins" must be responsible for the agglutination of the species *nasutus, truei, eremicus,* and *crinitus,* since these species are apparently devoid of the B factor. Likewise, the cells of *leucopus, gossypinus, maniculatus,* F_1 *maniculatus* × *polionotus* hybrids, and *polionotus* must possess some heteroagglutinogens, as is evidenced by the inability of group-B cells to exhaust group-A sera of their agglutinins against these species. Furthermore, the tests described in Tables I and II and Figure 1 suggest that the various *Peromyscus* species may vary in their capacity to absorb the heteroagglutinin fraction of group-A sera. A number of experiments were therefore performed to investigate this variation quantitatively.

TABLE III

AGGLUTINATION REACTIONS WITH PURIFIED ISOAGGLUTININ β

Cells	Dilution of β Agglutinin Solution							
	2^0	2^{-1}	2^{-2}	2^{-3}	2^{-4}	2^{-5}	2^{-6}	2^{-7}
Human group-B	++++	++++	+++	++	++	+	±	–
Beef (1)	++++	+++	++	+	±	–	–	–
Beef (2)	+++	+	±	±	–	–	–	–
leucopus	++++	+++	+++	+	+	±	±	–
gossypinus	++++	++++	+++	++	+	±	±	–
maniculatus (1)	++++	++++	+++	++	+	±	–	–
maniculatus (2)	++++	+++	++	+	±	–	–	–
maniculatus (3)	++++	++++	+++	++	+	±	–	–
F_1 *maniculatus* × *polionotus* hybrids	++++	++++	+++	++	+	±	±	–
polionotus	++++	++++	+++	++	±	–	–	–
nasutus	–	–	–	–	–	–	–	–
truei	–	–	–	–	–	–	–	–
eremicus	–	–	–	–	–	–	–	–
crinitus	–	–	–	–	–	–	–	–
Human group-O	–	–	–	–	–	–	–	–

Figure 2 illustrates the differences in absorptive capacity of nine different *Peromyscus* bloods against the heteroagglutinins of serum A–121. This serum, diluted 1:4, was twice absorbed with equal volumes of group-B cells in order to remove the β agglutinin. Parts of this solution were then treated with cells of the nine mice, using five different volumes of each blood. Single blood samples, rather than pools of several bloods of the same species, were used for the absorptions. The resulting solutions were then titrated against cells of a single *P. maniculatus blandus* mouse. Owing to these restrictions on the quantities of absorbed serum and test cells, it was not possible to test the preparations against cells of more than one species. If the results depicted in Figure 1 are typical, however, then it might be expected that similar sets of titration curves would have been secured with test cells of other species. A stock of *P. maniculatus blandus* was adopted as a standard source of test cells because of the high sensitivity of *maniculatus* cells as indicated by previous tests. Two other experiments, using other B-exhausted group-A sera absorbed with various *Peromyscus* bloods, gave results similar

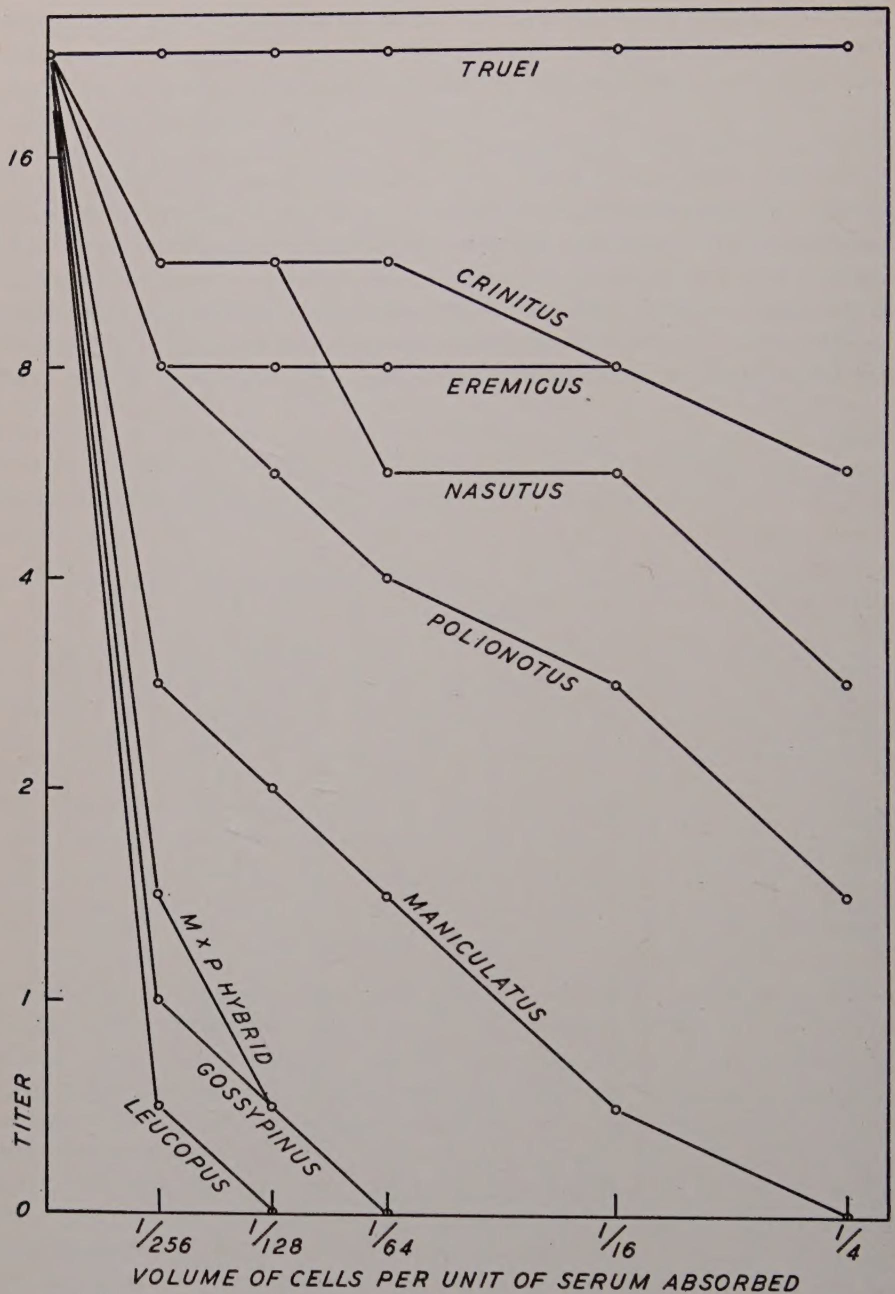

FIG. 2. Titration of the heteroagglutinin fraction of serum A–121 against cells of *Peromyscus maniculatus blandus*, after absorption with cells of various *Peromyscus* species.

to those of Figure 2. With the possible exception of *truei* and *nasutus,* the titration curves show species similarities which conform with the accepted taxonomic groupings.

DISCUSSION

B-like agglutinogens, reactive with human β agglutinin but not with anti-B agglutinins of immune rabbit sera, were regularly demonstrated by Landsteiner and Miller (1925) in New World monkeys (various species of *Cebus, Lagothrix, Mycetes, Chrysothrix,* and *Nyctipithecus*), as well as in the rabbit, guinea-pig, rat, mouse, cat, dog, cattle, donkey, and pig (von Dungern and Hirschfeld [1911], Landsteiner and Miller). Their presence has not thus far been observed in Old World monkeys (various species of *Papio, Cercopithecus, Cercocebus,* and *Macacus*), nor in the sheep, horse, or goat. Apparently, B-like antigens have been found in all rabbits and rodents thus far examined, with the exception of the four species of *Peromyscus* here reported. In contrast to the B agglutinogen of certain men, orangutans, and gibbons, the B-like antigens of the lower mammals appear to define specific differences rather than individual differences. It is of interest that the four *Peromyscus* species possessing the B factor are contained in the subgenus *Peromyscus,* whereas those lacking the factor belong to one cenospecies of the subgenus *Peromyscus* as well as to the subgenus *Haplomylomys.* Geographically, the B-negative group is confined largely to the southwestern part of North America. Unfortunately, there is no immediate prospect of investigating the genetics of this difference, since hybridization has not been observed between species belonging to these two groups (Dice, 1940).

For the genetical study of antigenic differences which are detectable with human heteroagglutinins, the two closely related species, *maniculatus* and *polionotus,* appear to offer the most promising material. A group-A serum exhausted of its anti-*polionotus* agglutinins still agglutinates cells of F_1 *maniculatus* × *polionotus* hybrids as well as cells of *maniculatus* (Table II). This might be explained by assuming that *maniculatus* mice possess one or more antigenic factors not present in *polionotus.* The presence of these factors in the hybrids would then be anticipated in accordance with a general rule of immunogenetics, namely, that genes determining the presence of antigens are dominant to those determining the absence of such antigens (or the presence of weaker antigens). In this connection, an agglutinogen reported by Gorer (1936) in certain strains of the house mouse is of interest. This property, which was demonstrable with human group-A sera (presumably with the heteroagglutinin fractions thereof), was shown to be determined by a single dominant gene. In Figure 2, the capacity of cells of the F_1 *maniculatus* × *polionotus* hybrid to absorb the heteroagglutinins against *maniculatus* cells is shown to exceed that of either parent species. This result has been observed in other tests and might suggest the inheritance of antigens from both species. The comparison of *blandus* and F_1 *maniculatus* × *polionotus* mice, however, is not entirely appropriate, since the former comprises a single subspecies of *maniculatus,* whereas the F_1 hybrids are offspring of *maniculatus* mice which are themselves hybrids of several subspecies. It is possible that these factors may show intraspecific variation, and the numerous subspecies of *maniculatus* and *polionotus* offer abundant material for further study.

It is of particular interest that the four *Peromyscus* species which react with the β agglutinin of group-A sera are also the four species which react most strongly with heteroagglutinins of the same sera (compare Table III and Figure 2). This correlation, which also appears to extend to variations within the B-positive group, suggests that the two agglutination systems may be chemically and genetically related. For example, it is conceivable that the same gene or genes may be responsible for major variations in both types of *Peromyscus* antigens. If so, the antigens reacting with at least some of the heteroagglutinins might be considered as special B components not contained in the human B complex. Friedenreich and With's (1933) interpretation of the human β agglutinin as a complex of several substances, some reactive only with human cells and some reactive with both human and animal cells, would thus be extended to include components reactive only with certain animal bloods. Further justification for this concept would be furnished if the heteroagglutinins of group-B sera should reveal antigenic differences between *Peromyscus* species unlike those demonstrated with group-A heteroagglutinins. Such comparative studies with human sera of groups B, O, and AB have not yet been made.

The two group-B sera (B–41 and B–518) that failed to agglutinate *Peromyscus* bloods, may also be of significance in relation to this problem. These two sera, which were provided by A. S. Wiener, were both obtained from group-B individuals who, by mistake, had received transfusions of group-A blood. The high isoagglutinin titers of these sera were therefore presumed to be due to the presence of immune α agglutinins in addition to the natural α agglutinins. The two sera were supplied in a dilution of 1 : 4, which may account for their negative reactions with *Peromyscus* cells. Even so, the heteroagglutinins against *Peromyscus* cells would be comparatively weak. It is therefore tempting to speculate that the formation of immune α antibodies may have resulted in a diminution of the animal heteroagglutinins in these sera.

Because of the interesting variations which have been observed in A and B substances of the body tissues and secretions of man and other animals, the testing of *Peromyscus* tissues is recommended for future study.

SUMMARY

Red blood cells of four species of North American mice, *Peromyscus leucopus, P. gossypinus, P. maniculatus,* and *P. polionotus,* possess an anti-

gen similar to the human isoagglutinogen B, whereas the cells of four other more distantly related species, *P. nasutus, P. truei, P. eremicus,* and *P. crinitus,* apparently lack this factor. The B-like antigen of *Peromyscus* is sufficiently similar to human B that it is activated by purified solutions of the human isoagglutinin β. On the other hand, like the B factors of other sub-primate mammals, it is not reactive with anti-human-B agglutinins of immune rabbit sera.

Human group-A sera also possess other agglutinins (heteroagglutinins) against which the cells of various *Peromyscus* species show quantitatively different reactions. Although the numbers of mice tested are small, the variability within species appears to be considerably less than that between species. It is therefore possible to differentiate cells of *maniculatus* and *polionotus* by means of group-A sera which have been absorbed by cells of *polionotus.* The absorptive capacity of the cells of the F_1 hybrids of these two species appears to at least equal that of the stronger parent, *maniculatus,* suggesting the inheritance of dominant factors from this species.

The reactivity of different *Peromyscus* species to the β agglutinin appears to be correlated with the reactivity against heteroagglutinins of the same sera. This suggests that the two systems of agglutination may bear chemical and genetical relationship. In both serological properties the similarities between *Peromyscus* species are in general consistent with taxonomic groupings within the genus.

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